REPRODUCTION IN THE CONIFEROUS FORESTS OF NORTHERN NEW ENGLAND[1]

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This investigation was undertaken to determine the factors governing the reproduction of the more important coniferous trees in the forests of northern New England. A detailed study of a single area was considered more effective than general observations over a wide area, but the study is not by any means exhaustive for the single area.

The work was done on Mount Desert Island, situated toward the eastern end of the coast of Maine, in about the same latitude as the northern part of the Adirondacks and northern New Hampshire. The island is included in the spruce region according to HAWLEY and HAWES (3). This is strictly correct; nevertheless, parts of the island show unmistakable signs of the more southerly white pine region. The location of the island is therefore of unusual interest. Being at the edge of the tension zone between two important regions, each with a distinct flora, there is a good opportunity to determine whether or not the northward migration of plants is still going on, and, if so, to study not only the rate of this migration, but also the many intricate factors involved in this phenomenon. Fortunately, about 5000 acres of this island have been made into a National Park, not only for purposes of recreation, but for scientific research in plant and animal ecology and in forestry.

The island is roughly 12 miles long by 15 miles wide, with a granite core running about northeast and southwest through its southern half. This granite has been cut across by glacial and water action in 9 places, so that instead of a continuous ridge we have a series of small mountains, 7 of them rising to over 1000 ft. above the sea. The northern slopes are gentle, the southern slopes

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are precipitous, due probably to water action during the post-glacial submergence (5). The northern half of the island is comparatively level. The topography therefore offers a diversity of habitats.

The climate of the island is a curious mixture of the marine and the inland, the former, of course, predominating, but the latter being found in places shut off from the ocean winds. On the northeast side of the island the average annual precipitation is 48.3 inches, of which 16.1 inches or one-third comes in the growing season (May–September inclusive). This should be abundant, but there are periods during the summer in which lack of moisture is an important factor.

The mean annual temperature is 44° F., running from 21° in January to 65.5° in July. The sea tends to keep the temperature uniform, but it is uniformly cold, for it is beyond the Gulf Stream. There are surprising fluctuations in temperature, however. The large areas of exposed granite rock take up and radiate great quantities of heat, so that the fluctuations, particularly in places cut off from the ocean winds, must have a distinct bearing on the vegetation.

The vegetation, although predominantly northern, contains a strong mixture of middle Atlantic elements. It contains not only plants but forest associations belonging to both the boreal and the transition zones (4). Furthermore, this island and Schoodic Point, a small peninsula about 10 miles to the eastward, are isolated stations for *Pinus divaricata*.

The forest associations of the island are 5 in number: (1) spruce, (2) white pine, (3) cedar, (4) pitch pine, (5) grey birch-aspen. Over most of the island, except the parts recently burned, the first 3 associations mingle in a rather confusing manner to form a forest containing varying proportions of red spruce, balsam fir, white pine, and white cedar, with an admixture of red maple, grey birch (giving place to paper birch and yellow birch on the cooler, moister sites), aspen, and occasionally red oak.

1. The spruce association is composed of nearly pure spruce, (*Picea rubens*), mixed with hemlock (*Tsuga canadensis*), balsam fir (*Abies balsamea*), white cedar (*Thuja occidentalis*), and white pine

(*Pinus Strobus*). It occurs on almost any site, even bare rock, provided there is moisture.

2. The white pine association, composed of nearly pure white pine, is not abundant. The association on Mount Desert, although predominantly white pine, contains a strong admixture of red spruce and cedar, and sometimes of red pine (*Pinus resinosa*). It occurs on somewhat drier sites than the spruce association.

3. The cedar association does not form as pure stands as the two preceding ones. Although cedar predominates numerically, there are generally considerable proportions of fir, spruce, and white pine, with red maple (*Acer rubrum*) and paper birch (*Betula papyrifera*). It occupies the moist flats.

4. The pitch pine (*Pinus rigida*) association, generally sharply separated from all others, is composed of pure pitch pine, or sometimes pitch pine and a little red pine. It occupies mostly the dry rocky southern exposures. On rocky flats not exposed to full isolation, white pine, fir, and spruce are creeping in under the pitch pine; on these flats, if not elsewhere, the pitch pine appears to be a pioneer association.

5. The grey birch-aspen (*Betula populifolia–Populus tremuloides* and *P. grandidentata*) association is temporary, following fires, and is replaced sooner or later by the original coniferous forest.

A striking feature of these forests, a feature common to many spruce forests in the west as well as in the east, is the preponderance of fir reproduction under the spruce, even when the parent stand is nearly pure spruce. It is unnecessary to go into the many hypotheses advanced to explain this. Perhaps the most widespread theory, and the one tried out in this investigation, is that the accumulation of acid in the soil under the spruce is detrimental to spruce and favorable to fir. COVILLE's work on the blueberry (2) shows that certain plants do require acidity in the soil. Could it be that fir is one of those plants, and that spruce, though tolerant of acid, is not positively benefited by it as the fir appears to be? To determine this point, seedlings of red spruce, balsam fir, and white pine were transplanted from the forest into 3 different kinds of soil. The shoots of these seedlings were measured every 5 days for growth in length. The seedlings were of approximately the same size and age, and were taken from the same place, so that variations due to size and vigor are eliminated. Each soil was placed in a flat approximately 8 cm. in depth, over which was placed a lath screen made so as to give half shade. All flats were in the open, were given no artificial watering after the first 2 days, and consequently were all under the same conditions except for the soil. These conditions were, furthermore, as close to natural forest conditions as possible.

The 3 soils were (1) A thoroughly decomposed forest humus which had been taken from the forest and rotted in a field for 2 years. This has a moisture-holding capacity, when saturated, of 138.5 per cent of its air-dry weight, or 82.6 per cent of its volume. (2) Undecomposed raw humus, taken directly from the spruce association, consisting of needles, cone scales, and other forest litter. This is COVILLE's "upland peat," the forest "duff" which accumulates in northern regions because decomposition is retarded by lack of sufficient warmth. Its moisture-holding capacity, saturated, is 504.6 per cent of its air-dry weight, but only 65.1 per cent of its volume. The high percentage of water on the basis of air-dry weight gives an idea of the extreme lightness of this raw humus. (3) Mineral soil from beneath the raw humus. This is a bouldery glacial till, a reddish brown sandy loam with but little clay (practically nothing remains in suspension after about an hour and a half). The moisture-holding capacity, saturated, is 66.8 per cent of the air-dry weight and 56.9 per cent of the volume.

It is regretted that the physical properties of the soils cannot be given in terms of the wilting coefficient. The reason is that it was impossible to make wheat or corn produce sufficient root systems in either the raw humus or the mineral soil. On the decomposed humus (soil [1] above) a single direct determination gave a wilting coefficient of 13 per cent. Calculations from the moisture-holding capacity at saturation, which are probably unreliable for these soils, gave, on the basis of volume, wilting coefficients of 21 per cent for the decomposed humus, 15 per cent for the raw humus, and 12 per cent for the mineral soil.

The acidity of each of these soils was tested by the method which COVILLE gives (**2**, pp. 26–28), and by the TRUOG method (**7**).

The decomposed humus was found to be neutral; the raw humus showed an acidity of 0.002 normal, and the mineral soil an acidity of 0.00017 normal by COVILLE's method. Yet by the TRUOG method the raw humus was strongly acid, and the mineral soil of medium acidity. Tests at the end of the growing season showed only a small diminution in acidity.

The measurements showed that the growth of both fir and spruce was most rapid on the mild humus, effectually disposing of the theory that acidity is required by fir, or favors the fir against the spruce. In fact, the difference in rate between the neutral and acid cultures was greater in fir than in spruce, indicating that spruce withstands acidity better than fir. Growth of both fir and spruce on the mineral soil was slightly more rapid than on the raw humus, except that toward the end of the season some of the spruces on the raw humus began a second growth period which enabled them to pass those on the mineral soil. White pine also did better on the mild humus than on the mineral soil; on the raw humus there were not enough trees of this species for definite conclusions.

The duration of the period of growth in length for the different species is interesting. Fir began elongating on June 1, and stopped on July 10, 40 days later; spruce and pine began on June 5, and did not stop until August 20, a period of 76 days, or nearly twice as long as that of fir. Some of the spruce on the raw humus showed a second growth period lasting until August 30; and yet fir, with its shorter growing period, is a faster growing tree than spruce.

An examination of the root systems of the different species on the different soils, made at the end of October, revealed some suggestive conditions. The roots of all 3 species in the mineral soil showed by far the poorest development. Yet the growth curves for the mineral soil show it to have been a little better than the raw humus. It may be that the nutrients contained by the raw humus are considerably less than in the mineral soil. The poor root development on the mineral soil is perhaps attributable to poor aeration. Since this was not a heavy soil, we have here another indication of the need for an ample oxygen supply on the part of the roots of these 3 conifers (1).

The roots of all species were thicker and thriftier looking on the raw humus than on the mild humus, although fir and white pine were a little more branched on the mild humus. Most striking of all, the roots of all 3 species on the raw humus were still capable of absorption, even at the end of October. This was shown by the presence of a considerable number of the little translucent growing tips which are found during the height of the growing season. On the mild humus growing tips capable of absorption were almost lacking except where the root came in contact with the wood of the flat. In the raw humus the root tips which had ceased to function became brown, while many of those on the mild humus became covered with a white fungus. A black fungus, common in the raw humus of the forest, was found attacking the roots on the mineral soil more than those on the raw humus, indicating that its presence may be due to low vigor on the part of the roots rather than to abundance of spores. The rootlets in the raw humus exhibited a propensity for searching out twigs and cones and growing through them.

Raw humus appears to have an effect on damping off fungus, quite the reverse of what might be expected. In an experiment to determine the effect of drying out, such as the raw humus is subjected to under natural conditions in the open, upon the germination and establishment of *Pinus resinosa*, it was found that on raw humus kept artificially moist there was no damping off, while on the raw humus which received no water except from rain the loss from damping off was 44.4 per cent of the seedlings germinating. That damping off should be so much worse on a dry than on a moist soil is contrary to all previous experience. The explanation is probably to be found in the great abundance of fungus spores in raw humus as compared with ordinary nursery soils, and in the much greater vigor and power of resistance on the part of the seedlings in the moist humus. It is also possible that the constant moisture held enough of the soil acid in solution to prevent germination of the damping off fungus spores, for it is known that treatment of nursery soils with acids before seeding, followed by ample watering during germination, diminishes the losses from damping off.

Experiments were also tried on the effect of these 3 soils on the growth of clover, wheat, and corn. Clover, as might be expected from its sensitiveness to acid, grew very poorly on the raw humus and mineral soil, but throve on the mild humus. In fact, it eventually died back and disappeared on the two former, lasting longer on the mineral soil than on the raw humus. Kubanka wheat did well on the mild humus, except for the shading, while on the raw humus and mineral soil it grew poorly. The dry weights per plant for Kubanka wheat sown June 24 and cropped September 15 were 0.53 gm. for the mild humus as against 0.08 gm. on the raw humus, and only 0.03 gm. on the mineral soil. Corn (Golden Bantam) did so well on the mild humus that it had to be removed to prevent interference with the other experiments, while on the raw humus it produced only 0.09 gm. dry weight per plant, and on the mineral soil 0.13 gm. after growing for more than 3 months. The corn, it will be noticed, did better on the mineral soil than on the raw humus, indicating that this plant is affected more by acidity than by poor aeration. On the other hand, wheat grew better on the raw humus than on the mineral soil; on the former it frequently died down but came up again, while on the latter it showed less power of recovery. This would indicate that wheat is less sensitive to acid than to poor aeration.

Field observations on the root systems of spruce, fir, and white pine showed that detailed studies of roots would probably yield interesting results. Spruce roots form a dense mat in the raw humus or "duff," a mat so dense that hardly a square centimeter under a spruce stand escapes. These rootlets keep growing toward the surface as the humus deepens, those in the lower layers dying back. Hence spruce is in a position to get the first water that reaches the forest floor. The quantity absorbed by these roots must be enormous, and cannot fail to be an important factor in reproduction. Fir roots are characteristically much less branched than those of spruce, and seem to go more into the mineral soil, though they also feed largely in the "duff." This greater penetration may possibly explain in part the ability of fir to grow on drier sites than spruce. White pine absorbs from both the raw humus and the mineral soil. The roots of all 3 species are often affected by a fungus which produces black threads of mycelium on the root tips. These threads prevent absorption and kill the portion of the root attacked. Yet seedlings appear thrifty even when a large proportion of their roots are affected in this way. Perhaps, since the fungus attacks only the smaller rootlets, the plant is able to develop new rootlets about as fast as the affected ones die off.

A factor of more importance than hitherto recognized is dryness due to the interception of precipitation by the crowns of spruce. The lack of vegetation under a forest of spruce has generally been attributed to lack of light. While light plays an important part, there are probably many cases where lack of moisture rather than lack of light is the determining factor. A rather striking illustration may be cited. Under the crown of a spruce growing in the open was found a patch of forest floor similar in every respect to the forest floor found under dense stands of spruce. Herbaceous vegetation and tree reproduction stopped abruptly at the edge of this spot, yet the crown of this tree was high enough to allow the ground under it to receive ample light. The only vegetation under the crown was a few grasses and asters, light demanding but comparatively drought resistant plants. The bareness of this piece of forest floor was due to lack of moisture, not to lack of light. This was confirmed by moisture tests, which showed that the soil beyond the crown, soil which had been giving up moisture to a thick herbaceous cover all summer and should consequently be drier than a spot which had given up nothing to vegetation and was not subject to high evaporation, possessed 59 per cent of moisture on the basis of air-dry weight as against 20.5 per cent under the crown of the spruce. On the basis of volume, which gives a better conception of the moisture relations in these light soils, the soil in the open contained 19 per cent of moisture as compared with 5.7 per cent under the crown. In another case in a spruce forest the moisture under a small opening in the canopy was 20.9 per cent by volume, as compared with 7.3 per cent under a spruce crown. In both of these cases the soil under the crown was powder-dry to the touch, while that beyond the crowns felt moist. It is evident, therefore, that under the crowns of spruce the soil is often so dry that neither reproduction nor herbaceous vegetation can become established, no matter how much light it receives.

Counts of the reproduction of spruce, fir, white pine, and cedar, correlated with age, showed that spruce, fir, and white pine become established only at intervals of several years, while cedar comes in every year. The cause of the failure of spruce and fir to become established every year is apparently not related directly to climatic factors, because the season of 1916 was unusually moist and favorable, yet practically no seedlings of these 2 species could be found. Probably the reason for this periodicity in spruce and fir reproduction is to be sought largely in the seed supply. White pine reproduced abundantly in 1916, so that climate can be eliminated as a factor; but since it is equally impossible to eliminate the matter of seed production, the periodicity of white pine reproduction may be due to both the season and the seed supply.

In fir there are indications of a periodicity of reproduction which is of considerably more importance than that due to the seed supply. Under many spruce stands which have reached about middle age, the fir reproduction is nearly all composed of large seedlings approximately 1–3 ft. in height; young seedlings are scarce. In these cases it appears that the fir came in profusely under a set of environmental conditions different from the present ones. Just what these conditions were it is impossible to say without further study. One of them may have been stronger light than at present. Indications of this were found in the fact that some of these cases of fir reproduction occur in stands which were formerly more open than they now are; also, small fir reproduction is abundant in young stands with a full but not very heavy canopy. That light is a factor would be in accordance with Zon's conclusion (**8**). Another factor may be decreasing moisture, due to the interception of precipitation by the crowns of the spruce trees, and to a fuller use of the humus water by the increasing mat of spruce roots. Whatever the factors are, it seems evident that fir reproduces within a more or less sharply marked range of environmental conditions, and that these conditions are largely controlled by the forest itself.

Each species reproduces only within a certain range of factors. This range is probably a specific characteristic of each tree, possibly of each plant, and appears to be different even for trees growing together in the same association.[2] Determination of this range for even a few of our more important trees would be a valuable contribution.

NEW YORK CITY

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[2] SHREVE (6) found that in open vegetation in Arizona the species growing in the same association are subject to different environments.